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Cephalopod prey of the wandering albatross *Diomedea exulans*

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Abstract

Cephalopod beaks from the stomach contents of "wandering albatross" (*Diomedea exulans* L.) chicks from Bird Island, South Georgia, were sampled between May and September in 1983 and 1984. Lower beaks were identified and measured, and allometric data were used to calculate mantle length and biomass of the species consumed. A total of 3 421 lower beaks were examined, representing 35 species in the 1983 sample and 45 species in the 1984 sample. Eight of the twenty families contributed over 95% of the biomass. In 1984 there were less Onychoteuthidae and more Ommastrephidae than in 1983 and a decrease in the number of species known to occur south of the Antarctic Polar Front. There was a difference in the size-frequency distribution of the cephalopod diet in the two years; in 1984 there was a higher frequency of intermediate-sized specimens, reflecting the greater importance of ommastrephids, especially *Illex* sp. The energy content of cephalopods in 1984 may have been greater than in 1983. Serial sampling of cephalopod beaks during the austral winter did not reveal evidence of growth. By the age of 200 d, wandering albatross chicks have consumed a total of approximately 100 kg wet weight of cephalopods each.

Introduction

The "wandering albatross", *Diomedea exulans,* has long been recognised as a predator of cephalopods in the Southern Ocean (Matthews, 1929). Adults and chicks accumulate considerable numbers of indigestible cephalopod beaks in the stomach, which can be sampled by inducing the bird to regurgitate. Recent advances in the identification of cephalopod beaks (Clarke, 1986) enable much information to be derived from these samples.

The first study of cephalopods in the diet of wandering albatrosses, based on seven samples (281 beaks), was made by Imber and Russ (1975). A more detailed study of 18 samples (532 beaks) was made by Clarke *et al.* (1981). Here, we describe serial collections of cephalopod material involving 3 421 lower beaks from 79 samples taken from chicks at the nest on Bird Island, South Georgia, during two breeding seasons, 1983 and 1984. Wandering albatrosses raise their chicks during the Antarctic winter (Tickell, 1968). These collections were separated by an Antarctic summer season, which was marked by a significant decline in standing-crop biomass of krill (*Euphausia superba*) in the vicinity of South Georgia (Heywood *et al.*, 1985). This was associated with reduced breeding success in the Macaroni penguins *Eudyptes chrysolophus,* the gentoo Penguins *Pygoscelis papua,* the black-browed albatrosses *Diomedea melanophris,* and, to a lesser extent, the grey-headed albatrosses, *D. chrysostoma* (Croxall *et al.*, in press). The breeding success of the wandering albatrosses was unaffected, but it was notable that the proportion of cephalopods in the diet decreased from 39.5% in 1983 to 29.7% in 1984; the difference being compensated for by fish in the second year (Croxall and Prince, personal communication).

Materials and methods

The stomach contents of wandering albatross (*Diomedea exulans* L.) chicks at the breeding colony on Bird Island, South Georgia were sampled at approximately monthly intervals between May and September 1983 and 1984. Samples were taken by inducing the chicks to regurgitate immediately after being fed by a parent bird. No chick was sampled more than once. All cephalopod beaks were removed from the samples and preserved in formalin. Lower beaks were identified by reference to features given by Clarke (1986).

Lower rostral length (LRL) of squid beaks and lower hood length (LHL) of octopodid beaks were measured to 0.1 mm with vernier calipers. Allometric equations given

by Clarke (1986) were used to relate LRL or LHL to original wet body weight and mantle length of the cephalopod. Where appropriate equations were not available, these were derived from new material (Rodhouse, unpublished data) or estimates were made from equations for closely related species or for species with similar morphologies.

Results

Taxonomic analysis of cephalopod prey

A total of 3 421 lower beaks were identified and measured from the regurgitations of *Diomedea exulans* chicks, 1 474 from the 1983 sample and 1 947 from the 1984 sample. Numbers of beaks from each cephalopod species and wet weight biomass represented by these beaks for each year are given in Table 1.

Identified cephalopod species are given here together with their contribution to diet as a percentage of total numbers and estimated percentage contribution to total cephalopod biomass. Where the contribution of a species to total numbers or weight is < 1%, data for both years are combined to derive size-frequency peaks.

Order Teuthoidea

Family Loliginidae

Loligo sp.

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 1.8 to 3.0 mm, peak at 2.0 to 2.5 mm.

Family Gonatidae

Gonatus antarcticus (Lonnberg, 1898)

In 1983 and 1984 this species contributed 2.6 and 2.4% by numbers and 1.2 and 1.0% by weight, respectively; LRL: 4.9 to 8.1 mm, peak at 6.0 to 7.0 mm in 1983 and at 5.5 to 6.0 mm in 1984 (Fig. 1). Clarke *et al.* (1981) found two peaks in LRL frequency within the same size range of *Gonatus antarcticus* lower beaks from wandering albatrosses. Beaks from the smaller group were ascribed to a second, unknown species by these authors. Here, we found no evidence of the smaller peak within this size range and so have provisionally assigned all *Gonatus* beaks to *G. antarcticus*.

Family Enoploteuthidae

Ancistrocheirus lesueuri (d'Orbigny, 1839)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 6.2 to 8.2 mm, peak at 7.5 to 8.0 mm.

Table 1. *Diomedea exulans.* Numbers of identified cephalopod beaks in regurgitations of chicks and wet weight biomass represented by these beaks

Family and species	Numbers		Biomass (g)	
	1983	1984	1983	1984
Loliginidae				
Loligo sp.	3	8	453	1 097
Gonatidae				
Gonatus antarcticus	38	47	10 726	10 893
Enoploteuthidae				
Ancistrocheirus lesueuri	2	3	2 359	2 960
Octopoteuthidae				
Octopoteuthis rugosa	1	0	214	0
Taningia danae	8	10	26 334	25 042
Onychoteuthidae				
Kondakovia longimana	192	151	555 209	617 961
Morotheuthis knipovitchi	47	14	36 817	9 482
Morotheuthis ingens	10	15	35 409	44 664
Morotheuthis robsoni	2	6	2 803	8 199
Onychoteuthis banksi	3	1	563	2 034
Pholidoteuthidae				
Pholidoteuthis boschmai	0	1	0	44
Batoteuthidae				
Batoteuthis skolops	36	51	1 073	1 356
Histioteuthidae				
Histiotheuthis sp. A	63	10	8 926	1 009
Histiotheuthis eltaninae	247	230	20 090	19 676
Histiotheuthis atlantica	62	113	13 683	18 720
Psychroteuthidae				
Psychroteuthis glacialis	52	15	5 097	1 786
? Large *Psychroteuthis*	6	7	4 524	3 960
Neoteuthidae				
Alluroteuthis antarcticus	88	76	35 425	28 939
Architeuthidae				
Architeuthis sp.	0	1	0	23 227
Ommastrephidae				
Illex sp.	165	648	53 137	208 781
Martialia hyadesi	45	75	15 917	25 738
Chiroteuthidae				
Chiroteuthis imperator	1	1	104	67
Chiroteuthis sp. (large)	11	3	436	247
Chiroteuthis sp. (small)	0	2	0	80
Chiroteuthis sp. A	6	1	527	57
Lepidoteuthidae				
Lepidoteuthis grimaldii	3	2	4 699	6 655
Mastigoteuthidae				
Mastigoteuthis sp. (large)	35	19	9 581	4 674
Mastigoteuthis sp. (small)	2	1	248	139
Mastigoteuthis sp. A	0	4	0	879
Cycloteuthidae				
Discoteuthis sp. (large)	3	5	1 046	1 515
Discoteuthis sp. (small)	5	2	615	249
Cranchiidae				
Egea inermis	0	1	0	78
Galiteuthis glacialis	273	358	2 440	30 735
Galiteuthis sp.	1	3	60	172
Helicocranchia sp.	2	1	58	28
Megalocranchia sp.	0	1	0	280
Mesonychoteuthis hamiltoni	0	3	0	628
Taonius pavo	13	5	3 775	1 483
Taonius sp.	24	16	6 215	4 230
Taonius sp B. (small)	0	2	0	278
Taonius sp B. (southern)	0	8	0	2 451
Teuthowenia sp.	2	3	655	816
Alloposidae				
Alloposus mollis	21	15	11 555	8 201
Octopodidae				
Large octopodid	0	5	0	11 144
Small octopodid	2	1	241	1 125
Vampyromorphidae				
Vampyroteuthis infernalis	0	1	0	77

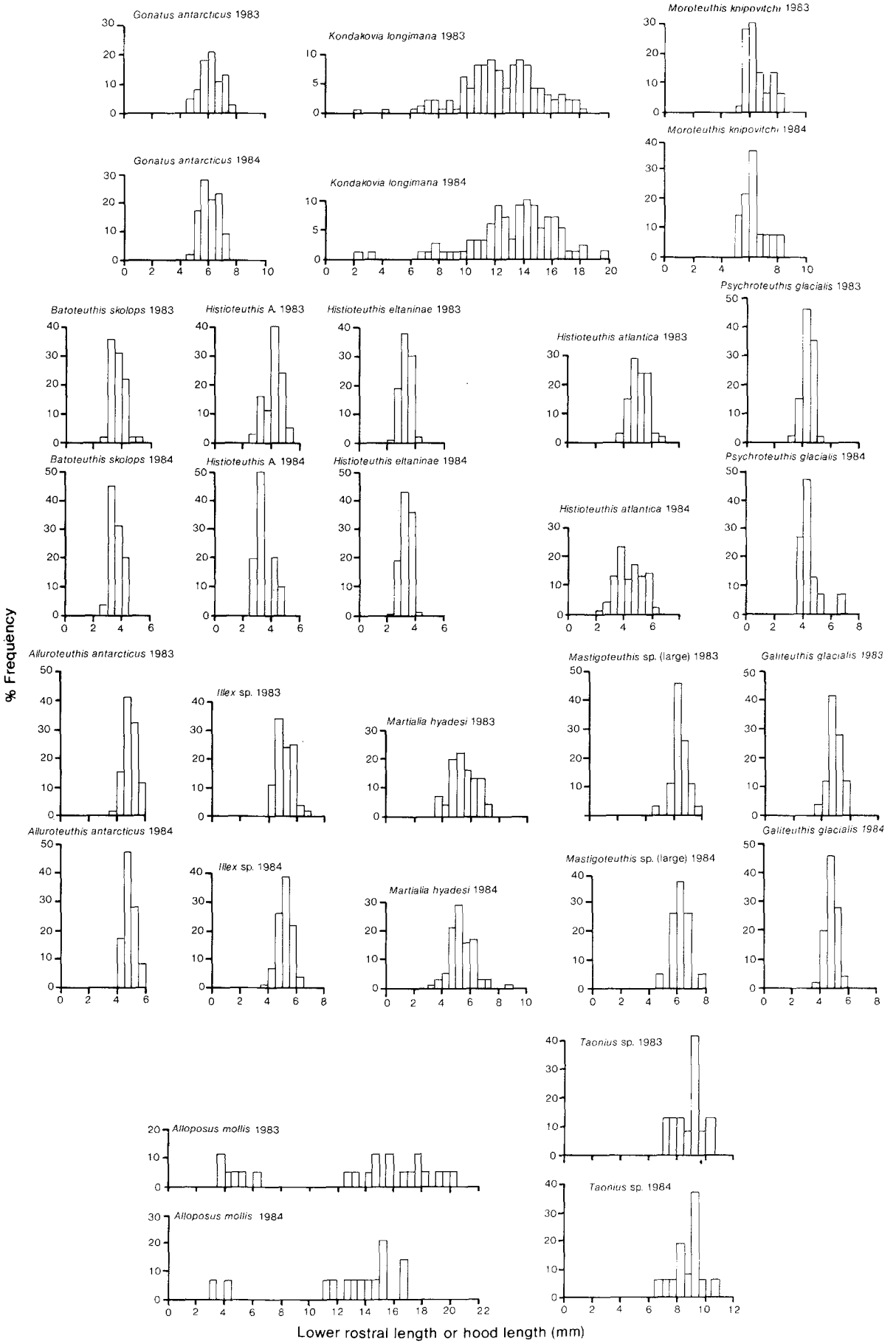

Fig. 1. *Diomedea exulans* chicks. Frequency distributions of lower rostral length and hood length for major cephalopod species in diet in 1983 and 1984

Family Octopoteuthidae

Octopoteuthis rugosa Clarke, 1980

One specimen in 1983; < 1% by numbers and weight; LRL: 9.5 mm.

Taningia danae Joubin, 1923

Present in 1983 and 1984; < 1% by numbers but 3.0 and 2.2% by weight, respectively; LRL: 9.0 to 15.7 mm, peak at 13.0 to 13.5 mm.

Family Onychoteuthidae

Kondakovia longimana Filippova, 1972

In 1983 and 1984 this species contributed 13.0 and 7.8% by numbers and 62.2 and 54.6% by weight, respectively; LRL: 2.3 to 20.0 mm, peak at 11.5 to 12.0 mm in 1983 and at 14.0 to 14.5 mm in 1984; evidence of a class of much smaller squids in each year (Fig. 1).

Moroteuthis knipovitchi Filippova, 1972

In 1983 and 1984 this species contributed 3.2 and 0.7% by numbers and 4.1 and 0.8% by weight, respectively; LRL: 5.2 to 15.3 mm, peak at 6.0 to 6.5 mm in 1983 and 1984 (Fig. 1).

Moroteuthis ingens (Smith, 1881)

Present in 1983 and 1984; < 1% by numbers but 4.0% each year by weight; LRL: 9.0 to 13.2 mm, peak at 10.0 to 10.5 mm.

Moroteuthis robsoni (Adam, 1962)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 7.6 to 8.5 mm, peak at 7.5 to 8.0 mm.

Onychoteuthis banksi (Leach, 1817)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 3.2 to 6.7 mm, peak at 3.5 to 4.0 mm.

Family Pholidoteuthidae

Pholidoteuthis boschmai Adam, 1950

One specimen in 1984, < 1% by numbers and weight; LRL: 2.7 mm.

Family Batoteuthidae

Batoteuthis skolops Young and Roper, 1968

In 1983 and 1984 this species contributed 2.4 and 2.6% by numbers, respectively, but < 1.0% by weight; LRL: 2.9 to 5.4 mm, peak at 3.0 to 3.5 mm in 1983 and 1984 (Fig. 1).

Family Histioteuthidae

Histioteuthis sp. A

In 1983 and 1984, beaks of *Histioteuthis* Type "A" (Clarke, 1986) contributed 4.3 and 0.5% by numbers and 1.0 and 0.1% by weight, respectively; LRL: 2.9 to 5.3 mm, peak at 4.0 to 4.5 mm in 1983 and at 3.0 to 3.5 mm in 1984 (Fig. 1). These peaks possibly represent different species. There is evidence of a smaller peak in 1983 which may correspond with the 1984 peak.

Histioteuthis eltaninae N. Voss, 1969

Beaks of *Histioteuthis* Type "B" (Clarke, 1986) were present in 1983 and 1984. There appear to be two distinct size groups. On this basis, and the stage of darkening, the smaller group was assigned to *H. eltaninae* and the larger group to *H. atlantica* (see Clarke *et al.*, 1981).

In 1983 and 1984, *Histioteuthis eltaninae* contributed 16.8 and 11.8% by numbers and 2.3 and 1.7% by weight, respectively; LRL: 2.5 to 4.5 mm, peak at 3.0 to 3.5 mm in 1983 and 1984 (Fig. 1).

Histioteuthis atlantica Hoyle, 1885

In 1983 and 1984 this species contributed 4.2 and 5.8% by numbers and 1.5 and 1.6% by weight, respectively; LRL: 2.5 to 6.7 mm, peak at 4.5 to 5.0 mm in 1983 and at 3.5 to 4.0 mm in 1984 (Fig. 1).

Family Psychroteuthidae

Psychroteuthis glacialis Thiele, 1921

In 1983 and 1984 this species contributed 3.5 and 0.8% by numbers but < 1.0% by weight; LRL: 3.5 to 6.6 mm, peak at 4.0 to 4.5 mm in 1983 and 1984 (Fig. 1).

? Large *Psychroteuthis*

Beaks assigned to this species come from an unknown squid which is possibly not related to the Psychroteuthidae (Clarke, 1986). It was present in 1983 and 1984; < 1% by numbers and weight; LRL: 4.2 to 7.9 mm, peak at 7.0 to 7.5 mm.

Family Neoteuthidae

Alluroteuthis antarcticus Odhner, 1923

In 1983 and 1984 this species contributed 6.0 and 3.9% by numbers and 4.0 and 2.6% by weight, respectively; LRL: 4.0 to 6.0 mm, peak at 4.5 to 5.0 mm in 1983 and 1984 (Fig. 1).

Family Architeuthidae

Architeuthis sp.

One specimen present in 1984; < 1% by numbers and weight; LRL: 13.3 mm.

Family Ommastrephidae

Illex sp.

This is probably *Illex argentinus* (Castellanos, 1960). In 1983 and 1984 it contributed 11.2 and 33.3% by numbers and 6.0 and 18.4% by weight, respectively; LRL: 3.3 to 8.2 mm, peak at 4.5 to 5.0 mm in 1983 and at 5.0 to 5.5 mm 1984 (Fig. 1).

Martialia hyadesi Rochbrune and Mabille, 1889

In 1983 and 1984 this species contributed 3.1 and 3.8% by numbers and 1.8 and 2.3% by weight, respectively; LRL: 3.5 to 8.8 mm, peak at 5.0 to 5.5 mm in 1983 and 1984 (Fig. 1).

Family Chiroteuthidae

Chiroteuthis imperator Chun, 1910

One specimen present in 1983 and 1984; < 1% by numbers and weight; LRL: 6.1 and 5.2 mm, respectively.

Chiroteuthis sp. (large)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 3.4 to 6.8 mm, peak at 3.0 to 3.5 mm.

Chiroteuthis sp. (small)

Two specimens present in 1984; < 1% by numbers and weight; LRL: 2.9 and 4.9 mm.

Chiroteuthis sp. A

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 4.3 to 8.2 mm, peak at 4.5 to 5.0 mm.

Family Lepidoteuthidae

Lepidoteuthis grimaldii Joubin, 1895

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 9.1 to 15.8 mm, peak at 7.5 to 8.0 mm.

Family Mastigoteuthidae

Mastigoteuthis sp. (large)

In 1983 and 1984 this species contributed 2.4 and 1.0% by numbers and 1.0 and 0.4% by weight, respectively; LRL: 4.8 to 7.9 mm, peak at 6.0 to 6.5 mm in 1983 and 1984 (Fig. 1).

Mastigoteuthis sp. (small)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 5.0 to 5.2 mm, peak at 5.0 mm.

Mastigoteuthis sp. A

Four specimens present in 1984; < 1% by numbers and weight; LRL: 5.9 to 6.2 mm, peak at 6.0 to 6.2 mm.

Family Cycloteuthidae

Discoteuthis sp.

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 6.7 to 7.8 mm, peak at 7.0 to 7.5 mm.

Discoteuthis sp. (small)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 4.1 to 4.9 mm, peak at 4.0 to 4.5 mm.

Family Cranchiidae

Egea inermis Joubin, 1933

One specimen present in 1984; < 1% by numbers and weight; LRL: 5.1 mm.

Galiteuthis glacialis (Chun, 1906)

In 1983 and 1984 this species contributed 18.5 and 18.4% by numbers, respectively, and 2.7% each year by weight; LRL: 3.2 to 6.4 mm, peak at 4.5 to 5.0 mm in 1983 and 1984 (Fig. 1).

Galiteuthis sp. (see Clarke, 1986: his Fig. 99 D)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 4.0 to 4.2 mm, peak at 4.0 to 4.2 mm.

Helicocranchia sp.

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 3.0 to 3.5 mm, peak at 3.0 to 3.5 mm.

Megalocranchia sp.

One specimen in 1984; < 1% by numbers and weight; LRL: 8.2 mm.

Mesonychteuthis hamiltoni Robson, 1924

Three specimens in 1984; < 1% by numbers and weight; LRL: 5.9 to 10.0 mm.

Taonius pavo (Lesueur, 1821)

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 7.0 to 10.5 mm, peak at 9.0 to 9.5 mm.

Taonius sp.

In 1983 and 1984 this species contributed 1.6 and 0.8% by numbers and weight, respectively; LRL: 7.0 to 11.0 mm, peak at 9.0 to 9.5 mm in 1983 and 1984 (Fig. 1).

Taonius sp. B (small)

Two specimens in 1984; < 1% by numbers and weight; LRL: 6.5 and 6.8 mm, respectively.

Taonius sp. B (southern)

Eight specimens in 1984; < 1% by numbers and weight; LRL: 7.9 to 9.9 mm, peak at 9.5 to 10.0 mm.

Teuthowenia sp.

Present in 1983 and 1984; < 1% by numbers and weight; LRL: 7.0 to 9.0 mm, peak at 8.0 to 8.5 mm.

Order Octopoda
Family Alloposidae

Alloposus mollis Verrill, 1880

In 1983 and 1984 this species contributed 1.4 and 0.8% by numbers and 1.3 and 0.7% by weight, respectively; LHL: 3.5 to 21.0 mm, peaks at 3.5 to 4.0 mm and 15.5 to 16.0 mm in 1983 and at 3.0 to 4.5 mm and 15.0 to 15.5 mm 1984 (Fig. 1).

Octopodidae

In 1984 there were five beaks from large unidentified octopodids; < 1% by numbers but 1.0% by weight; LHL: 5.4 to 11.4 mm; no size-frequency peak. In 1983 there was one small octopodid; < 1.0% by numbers and weight; LHL: 3.8 mm. In 1984 there were two small octopodids; < 1.0% by numbers and weight; LHL: 4.8 and 5.4 mm.

Order Vampyromorpha
Family Vampyromorphidae

Vampyroteuthis infernalis Chun, 1903

In 1984 there was one beak from this species; < 1.0% by numbers and weight; LHL: 7.0 mm.

Contribution to diet of different cephalopod families

Of the twenty cephalopod families represented in the collection (Table 1), eight families contributed 95.6% of the biomass consumed. The other families each contributed < 1.0%. The percent biomass contributed by the eight most important families in each of the two years is shown in Fig. 2. The relative contribution of each of these eight families was similar in each year except for the Onychoteuthidae and the Ommastrephidae. There was a decrease in importance of the Onychoteuthidae and an increase in the Ommastrephidae in 1984. This was largely due to an increase in the numbers and biomass of *Illex* sp. and a decrease in the numbers and biomass of *Kondakovia longimana* and *Moroteuthis knipovitchi* in 1984 (Table 1 and Fig. 3).

Relative contribution of "Antarctic" and "non-Antarctic" cephalopod species

Although the distribution of cephalopods in the Southern Ocean is poorly known, some measure of the relative importance of "Antarctic" and "non-Antarctic" species was derived by classifying the collection according to known occurrence to the south of the sub-Antarctic Front (SAF) (Fischer and Hureau, 1985; Okutani and Clarke, 1985).

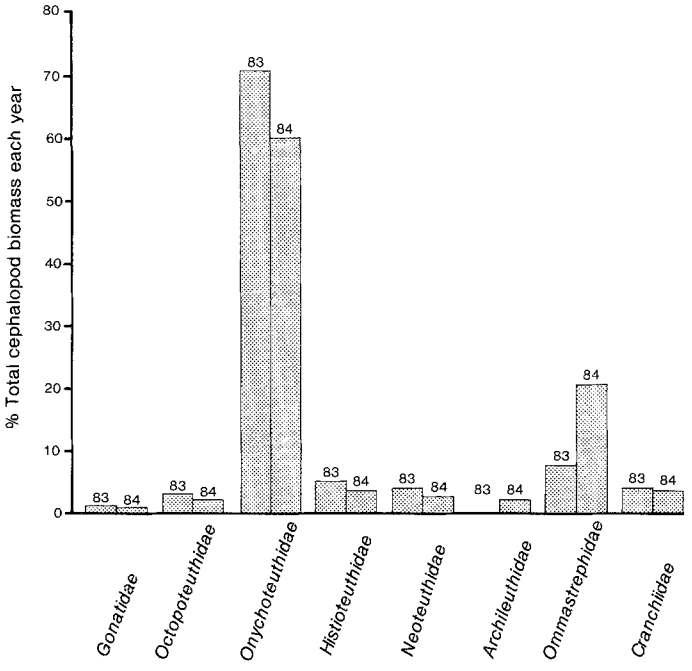

Fig. 2. *Diomedea exulans* chicks. Relative contribution of each of 8 most important cephalopod families to diet in 1983 and 1984

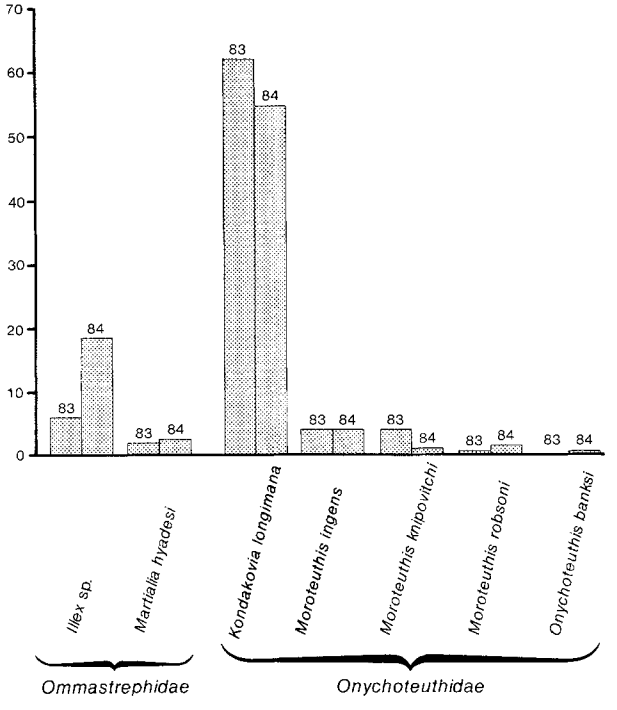

Fig. 3. *Diomedea exulans* chicks. Relative contribution of ommastrephid and onychoteuthid species to diet in 1983 and 1984

Species defined here as "Antarctic", with a known distribution south of the SAF, are: *Gonatus antarcticus, Kondakovia longimana, Moroteuthis knipovitchi, M. ingens, M. robsoni, Batoteuthis skolops, Psychroteuthis glacialis,* ? large *Psychroteuthis, Martialia hyadesi, Chiroteuthis* sp., *Mastigoteuthis* sp. A, *Galiteuthis glacialis* and *Mesonychteuthis hamiltoni.* The relative contribution of "Antarctic" and "non-Antarctic" species is given in Table 2. There

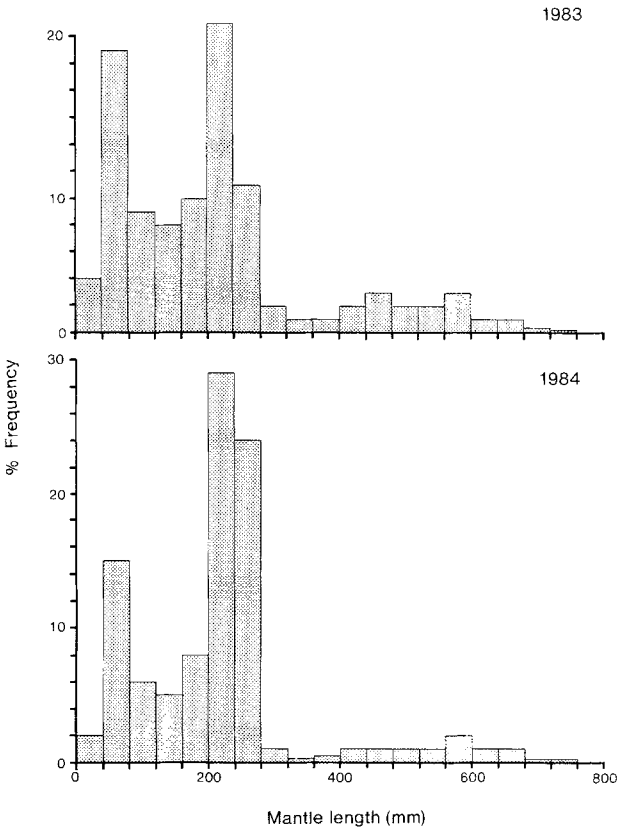

Fig. 4. *Diomedea exulans.* Pooled data of estimated mantle-length frequency-distributions of all cephalopods from regurgitations of chicks in 1983 and 1984

Table 2. *Diomedea exulans* chicks. Relative contribution (%) of "Antarctic" and "non-Antarctic" cephalopods to diet

Year	"Antarctic"	"non-Antarctic"
Numbers		
1983	54	46
1984	42	58
Biomass		
1983	81	19
1984	69	31

was a marked reduction in the contribution of "Antarctic" species, in terms of species and biomass, to the diet of wandering albatrosses in 1984.

Size-frequency distribution of cephalopod prey

Frequency distributions of estimated mantle lengths, combined for all species in the 1983 and 1984 collections are shown in Fig. 4. The general form of the distribution is very similar in both years, with major peaks at 40 to 80 mm, 200 to 240 mm and 560 to 600 mm mantle length. However, it is notable that in 1984 the relative importance of the peaks at each end of the distribution are reduced relative to the major peak at 200 to 240 mm. This reflects the increased number of *Illex* sp. fed to chicks in 1984.

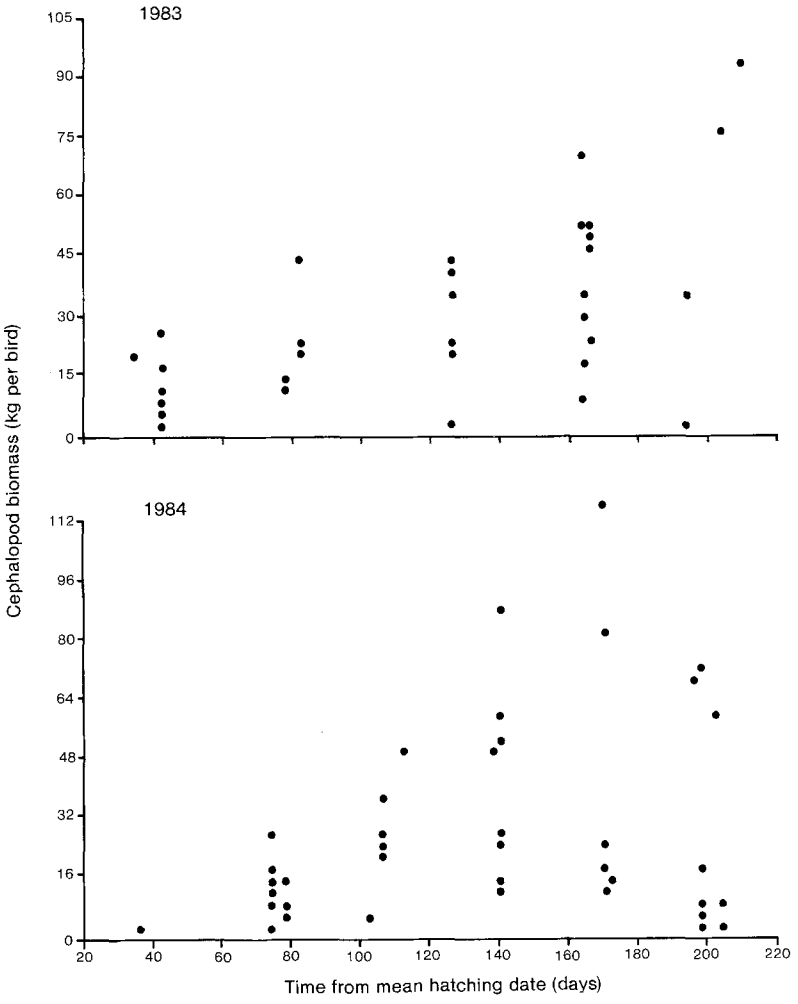

Fig. 5. *Diomedea exulans.* Wet weight biomass represented by cephalopod beaks regurgitated by chicks, as a function of time after mean hatching date in 1983 and 1984. Data points represent individual chicks

Accumulation of cephalopod beaks

The estimated biomass represented by beaks regurgitated by each chick, as a function of time after mean hatching date, is shown in Fig. 5. Mean hatching dates were 12 March 1983 and 10 March 1984. In both years there was a general increase in biomass during the early months of the life of the chick, but thereafter the data became increasingly variable. This suggests that, as development progresses, cephalopod beaks are lost from the chicks stomach, either in regurgitations or in the faeces, or that it becomes more difficult to recover all cephalopod beaks from the older, larger chicks. Maximum estimates of the biomass of cephalopods consumed by chicks are 70 to 90 kg in 1983 and 80 to 110 kg in 1984. These values will be overestimates to the extent that not all beaks will have come from whole cephalopods, but underestimates by the amount of cephalopods still to be delivered before the chicks fledge at 260 to 280 d of age and by the number of beaks consumed but not recovered from the chick.

Despite these potential sources of error, it seems possible that chicks ingest up to 100 kg of cephalopods each during the rearing period. This is not unrealistic because between the end of the brooding period and fledging, chicks receive about 80 meals (Tickell, 1968) of 1 to 2 kg (Tickell, 1968; Croxall and Prince, unpublished data) of which about 35% by weight is cephalopods (Croxall and Prince, unpublished data). Thus, the average chick should receive in excess of 30 to 60 kg of cephalopods during the rearing period.

Cohort analysis

Four squid species were sufficiently common throughout the sampling periods in both years for cohort analysis of the LRL frequency distributions. These were the "Antarctic" species *Kondakovia longimana* and *Galiteuthis glacialis* and the "non-Antarctic" species *Illex ? argentinus* and *Histioteuthis eltaninae.* There is no evidence of temporal shifts in peaks of these distributions which could be attributed to growth.

Heterogeneity of species-frequency

A two-way contingency table classified by species and year was drawn up to test for heterogeneity of species-frequency between years. The sixteen most common species were allocated separate columns in the table, with the remaining

thirty species grouped into one column. A log-linear model was fitted to the table as described by Nelder and McCullagh (1983). The residual deviance which is distributed as χ^2, indicated that there were considerable changes in relative frequency of species between the two years ($P < 0.001$).

Index of diversity

The Shannon-Wiener index of diversity (Pielou, 1966) was calculated for each year separately and both years combined. The value for 1983 was 2.619 and for 1984 it was 2.287; for both years combined it was 2.495. Associated values for eveness were 0.731, 0.697 and 0.648, respectively.

Discussion

A total of forty-six cephalopod species were identified from beaks in the regurgitations of wandering albatross (*Diomedea exulans*) chicks, sampled during the austral winter. This is nearly twice as many as recorded by Clarke *et al.* (1981) from chicks sampled at the same site, but the present collection was larger and more comprehensive. In common with the earlier study, the large hooked squid *Kondakovia longimana* dominated the sample in terms of biomass but not in numbers. Most of the species in this study which were not found by Clarke *et al.* (1981) were only present in small numbers, with the exception of the arrow squids *Illex* sp. and *Martialia hyadesi*. These species were sufficiently abundant to make the Ommastrephidae the second most important family in the diet in terms of biomass.

The 1984 sample contained ten more species than the 1983 sample, but the index of diversity decreased slightly. The additional species in 1984 were sufficiently rare as to make very little contribution to the index. Indeed, their presence in the sample caused the calculated measure of eveness (Pielou, 1966) to decrease. Therefore, their occurrence did not increase the degree of uncertainty attached to the specific identity of any randomly selected individual.

Comparison with the data from 1976/1977 (Clarke *et al.*, 1981) shows that in Clarke's study, fewer warm-water species were taken by the wandering albatrosses than in either 1983 or 1984. However, the data for 1983 are more similar to those of 1976/1977 than the 1984 data.

The species composition and relative frequency of species showed some striking differences between the two years 1983 and 1984. Thirty-five species were recorded in 1983; forty-five were recorded in 1984. Of the ten species confined to 1984, one was *Mesonychteuthis hamiltoni*, a deep-living Antarctic species which grows to a large size (Rodhouse and Clarke, 1985) and which only occasionally occurs in the diet of albatrosses (Clarke and Prince, 1981; Clarke *et al.*, 1981). The other nine species are all presumed to come from warmer water north of the SAF. Two species, *Egea inermis* and *Megalocranchia* sp. are thought to have tropical/sub-tropical distributions (Voss, 1974, 1980). This suggests than in 1984 a more northerly cephalopod community was available to the birds, either because their foraging range (see Croxall *et al.*, 1984) was extended, or because of a southerly incursion of water from the south Atlantic Ocean. It seems likely that the environmental conditions which caused the krill failure in the austral summer of 1983/1984 (Heywood *et al.*, 1985) also influenced the cephalopod community available to wandering albatrosses in 1984.

Availability of warmer-water cephalopods in 1984 is reflected by the increase in the albatross diet of *Illex* sp. from 11 to 33% by numbers. The nearest known stock of *Illex* to South Georgia is *I. argentinus*, which occurs over the Patagonian shelf (Roper *et al.*, 1984). It is possible that the increase in ommastrephids in the diet changed the energy content of the food delivered to the chicks, because those onychoteuthids which store ammonium as a buoyancy mechanism (Clarke *et al.*, 1979) have lower energy contents than ommastrephids (Clarke *et al.*, 1985). Thus, if it is assumed that *Kondakovia longimana* has the same energy content as *Moroteuthis robusta* and *Illex* sp. has the same energy content as *Todarodes sagittatus*, then the energy content of the cephalopod diet in 1984 would have increased by 9.6% as a result of increased consumption of *Illex* sp.

Elsewhere, Offredo *et al.* (1985) have been able to demonstrate shifts in size-frequency peaks of squid beaks taken from the stomachs of Antarctic vertebrate predators during the austral summer. In the present study, those species numerous enough through time to be amenable to analysis showed no evidence of growth. The present study was conducted during the austral winter, and the data suggest that growth rate, at least in the commoner species, is much reduced during the period May to September.

Clarke *et al.* (1981) pointed out that several of the families of cephalopod consumed by wandering albatrosses were previously thought to be deep-living. Recent data on vertical distribution of squid, as sampled by nets in the Antarctic (Rodhouse and Clarke, 1985, 1986; Rodhouse, in press), confirm that for three species known to be consumed by wandering albatrosses the usual distribution of larger specimens is considerably deeper than the depths at which the birds could possibly capture their prey. Furthermore, in two species for which there is sufficient data, *Alluroteuthis antarcticus* and *Galiteuthis glacialis*, there is evidence of ontogenetic descent. Whilst we still maintain that seabirds probably consume the remains of cephalopods regurgitated by whales (Clarke *et al.*, 1981), the question of whether other sources of cephalopods are available must be addressed. Given that ontogenetic descent occurs in several squid species, including some from the Antarctic, there is clearly a return towards the surface at some phase in the life cycle. Eggs may be laid at depth and float towards the surface, hatchlings may hatch at depth and migrate towards the surface, or adults may migrate towards the sur-

face to mate and/or spawn. Given that many species of cephalopods are semelparous and die after spawning (see Boyle, 1983), if mating/spawning migrations towards the surface followed by mass mortalities do occur, then these aggregations would represent considerable, but sporadic, opportunities for surface-foraging seabirds. The adult size at reproduction of Antarctic cephalopods is not known, so the present data cannot support this hypothesis. However, it is notable that there is a relatively small size range of beaks from most cephalopod species in the regurgitations of wandering albatross chicks.

It has been proposed by Imber and Russ (1975) that wandering albatrosses feed mostly at night and detect cephalopod prey through their bioluminescence. We adhere to the view expressed by Clarke *et al.* (1981), that this is unlikely because the light organs of most species are screened in such a way as to be invisible from above (Young, 1977).

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